An assessment of behavioural syndromes in rangeland-raised beef cattle

Robert L. Wesley [b], Andrés F. Cibils [a,*], J. Travis Mulliniks [a], Emily R. Pollak [b], Mark K. Petersen [c], Ed. L. Fredrickson [d,1]

[a] Department of Animal and Range Science, Box 30003, MSC 3-I, New Mexico State University, Las Cruces, NM 88003, USA
[b] Red Canyon Ranch, The Nature Conservancy, Lander, WY 82520, USA
[c] USDA-ARS Fort Keogh Livestock and Range Research Laboratory, 243 Fort Keogh Rd., Miles City, MT 59301, USA
[d] USDA-ARS Jornada Experimental Range, P.O. Box 30003, MSC 3JER, Las Cruces, NM 88003, USA

ARTICLE INFO

ABSTRACT

Individuals in most animal groups exhibit consistent behavioural differences across situations or over time known as behavioural syndromes. We conducted a study with a herd of young rangeland-raised cows to determine whether animals exhibited consistent differences in foraging behaviours across contexts (confinement vs. rangeland pasture) and could be clustered into behavioural type groups on the basis of a suite of correlated behaviours. We also investigated whether cows with different behavioural types performed differently in this environment. Supplement consumption rate (SCR) in confinement was used to select two groups of cows (*fast eaters* vs. *slow eaters*). This classification was validated by measuring the persistence of SCR differences through time, conducting cluster analysis to classify individuals into two behavioural types (BT_1 and BT_2) on the basis of a suite of 14 behavioural, physiological, and performance predictors, and comparing serum cortisol concentrations of cows in either group. Discriminant and linear correlation analyses were used to assess the influence of behavioural and performance responses on the classification of cows, and to study the relationships between behaviour and animal performance. Thirty-three young cows were tracked with GPS collars for approximately 45 days during the calving seasons of 2006 and 2007 and several performance responses were measured on each individual. Cows classified as exhibiting BT_1 had significantly higher ($P \le 0.05$) SCR (mean $\pm$ SE 2006: 1.90 ± 0.1; 2007: 2.54 ± 0.1 g/s) and serum cortisol (SC) concentrations (8.8 ± 0.88 ng/mL) than BT_2 counterparts (SCR 2006: 0.32 ± 0.03 g/s; SCR 2007: 1.59 ± 0.1 g/s; SC: 5.5 ± 0.5 ng/mL). Compared to BT_2 cows, BT_1 individuals tended to spend less time at water (BT_1: 73 ± 10; BT_2: 172 ± 16 min/day), cover larger areas (BT_1: 21 ± 0.3; BT_2: 17 ± 2 ha/day), and exhibit less concentrated search patterns (BT_1: 264 ± 8.9; BT_2: 314 ± 2 6 m travelled/(ha covered/day)). BT_1 individuals tended to be heavier (BT_1: 434 ± 7; BT_2: 394 ± 10 kg) and began gaining weight sooner after calving (BT_1: 44 ± 3; BT_2: 69 ± 6 days). Cows exhibiting BT_1 were more abundant in the herd and appeared to perform better in the rangeland environment where we conducted the study. Further research is needed to determine the constraints imposed by this behavioural syndrome on animal performance in other feeding environments.

Published by Elsevier B.V.

---

* Corresponding author. Tel.: +1 505 646 4342; fax: +1 505 646 5441.
E-mail address: acibils@nmsu.edu (A.F. Cibils).
[1] Current address: Department of Agriculture, Eastern Kentucky University, Richmond, KY 40475, USA.

1. Introduction

Consistent animal to animal differences in behaviour within and across contexts (or time) are known as behavioural syndromes (Sih et al., 2004a,b). Unlike the closely related concepts of animal temperaments (Réale et al., 2007), personalities (Bell, 2007a; Gosling, 2001; Stamps and Groothuis, 2010), or coping styles (Koolhaas et al., 2007, 2010, 1999), the definition of behavioural syndromes is broader and includes correlated suites of both inherited and learned behaviours which need not exhibit lifelong constancy (Sih and Bell, 2008). The study of behavioural syndromes allows insights into how an individual's foraging behaviour, for example, is correlated with its behavioural patterns in other contexts (e.g., maternal behaviours, predator avoidance) and provides a means of understanding the behavioural constraints limiting an animal's ability to adapt to changes in its environment (Bell, 2007b). Because behavioural syndromes are of consequence to an individual's fitness (Smith and Blumstein, 2008) this approach to studying individual variation in correlated behaviours could be a valuable means of explaining animal to animal productivity differences in agricultural settings.

Although the concept of behavioural syndromes has never been formally applied to livestock, there is a vast body of literature dealing with the study of beef cattle temperaments in relation to a variety of animal- and environment-related factors. The connections between temperament and individual weight gains (Petherick et al., 2009b; Voisinet et al., 1997b), carcass quality (Hall et al., 2011; Voisinet et al., 1997a), levels of stress hormones (Curley et al., 2006, 2011), faecal pathogen loads (Schuehle Pfeiffer et al., 2009) or phenotypic traits such as facial hair whorls (Grandin et al., 1995; Olmos and Turner, 2008) or eye white percentage (Core et al., 2009) have been studied in depth. Despite this, most of these studies have been somewhat narrowly focused on only the first of five general temperament trait categories (shyness–boldness, exploration–avoidance, activity, sociability, aggressiveness) described by Réale et al. (2007). The tendency to focus on shyness–boldness reactions involving fear-eliciting stimuli (including humans) is not surprising given that beef cattle temperament studies usually involve feedlot settings where human contact and animal handling is frequent. In rangeland environments, however, exploration–avoidance dimensions of livestock temperaments (Réale et al., 2007) may be as important as shyness–boldness reactions, given the ever-changing nature of forage resources. No studies to the best of our knowledge have addressed these dimensions of beef cattle temperaments on rangelands.

Correlations among temperament traits and their connections with animal performance measures have been studied in relation to animal handling regimes (Petherick et al., 2009a) and genotype (Benhajali et al., 2010; Gutiérrez-Gil et al., 2008; Nkrumah et al., 2007a). Yet, again, these studies have focused mostly on the relationship between traits that express shyness–boldness reactions to risk (Réale et al., 2007) and have seldom investigated consistency in animal to animal variations across contexts.

The behavioural syndrome approach to studying individual variation in correlated behaviours is particularly valuable because it allows animals to be classified into behavioural type categories (Luttbeg and Sih, 2010) on the basis of multiple behavioural traits encompassing several of the five temperament categories described by Réale et al. (2007). In addition, this approach focuses on detecting consistent variations in correlated behaviours not only through time (commonly measured in livestock temperament studies) but also across contexts (Bell, 2007b). Because of this, we agree with Searle et al. (2010) that in rangeland environments "behavioural syndromes offer a potentially valuable way to identify individuals with traits of benefit to particular environments or management goals" (Searle et al., 2010, p. 9).

The four most common approaches to studying behavioural syndromes according to Bell (2007b) include the 'puzzling behaviour', 'candidate behaviour', 'bottom-up' or 'proximate perspective', and the 'ecological' approach. The first strategy studies how an intriguing behaviour of a given species correlates with its behaviours in other contexts and seeks to understand the costs and benefits of the syndrome across contexts. The second strategy consists of identifying relationships between behaviours previously shown to constitute a behavioural syndrome in other animal species. The third approach begins by identifying a suite of behaviours assumed to be controlled by the same neuroendocrine or genetic system and studies correlations among such behaviours across different contexts. The last approach consists of identifying correlated behaviours that explain differences in fitness of individuals in a population. All behavioural syndrome studies regardless of the approach followed must include a group of animals that exhibit behavioural variation and whose individual behaviour is measured multiple times in a variety of contexts (Bell, 2007b).

We conducted a 2-year study of behavioural syndromes among approximately one-hundred and sixty 2- and 3-yr-old rangeland-raised beef cows (80/yr) to determine whether: (a) animals exhibited consistent differences in foraging behaviours across contexts (confinement vs. rangeland pasture); (b) animals could be clustered into behavioural type groups on the basis of a suite of behavioural and physiological parameters; (c) the behavioural traits measured were correlated; and (d) behavioural type groups could be discriminated on the basis of a suite of performance measures. Our study followed two of the four established behavioural syndrome research approaches described above. First, using the puzzling behaviour strategy (Bell, 2007b) we determined whether cows that consistently exhibited conspicuously slow or rapid supplement consumption rates in confinement differed in their rangeland pasture use patterns and whether there were animal performance-related costs associated with each syndrome. Second, we used the ecological approach (Bell, 2007b) to determine whether grazing and social behaviours were correlated with four important livestock performance (fitness) traits that are of economical and ecological consequence to cow–calf operations on rangelands.

2. Materials and methods

2.1. Study site

Our study was conducted at the New Mexico State University Corona Range and Livestock Research Centre (CRLRC; Lat 34°15′36″N, Long 105°24′36″W) in central New Mexico, USA. The CRLRC has an average elevation of 1900 m and a mean annual precipitation of 397 mm, with more than one-half the rainfall typically received as short duration convectional thunderstorms between July and September. The coldest month is January with an average minimum temperature of −5 °C; the hottest month is typically July with an average maximum temperature of 29 °C.

All animals in the study grazed a 146 ha pasture (Fig. 1) which included four major soil associations with vegetation composed of perennial grassland with an overstory of sparse to dense piñon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) woodlands. Approximately 82 ha of the pasture were covered with dense to sparse piñon/juniper (PJ) woodland with the remainder being open grassland with a low density of small (<3 m) juniper saplings. Drinking water was available from a single source located at the far west corner of the pasture.

2.2. Animals and classification protocol

All animal handling and experimental protocols were in accordance with the New Mexico State University Institutional Animal Care and Use Committee. Thirty-six 3-year old rangeland-raised lactating cows that were primarily Angus × Hereford and Angus breeding weighing 426 ± 7 kg (mean ± SE) were used in this 2-year study (2006 and 2007). Each year, 18 different cows were selected from a pool of approximately eighty 2- and 3-yr-old lactating cows that were part of a postpartum protein supplementation study (Mulliniks et al., 2011). Cows in our study (*n* = 18 each year) continued receiving supplements twice-weekly but grazed a separate pasture (described above) for the length of the experiment. On feeding days, cows were gathered after their morning grazing bout, sorted from their calves and moved into the feeding stalls to receive supplements. After consuming supplement, cows were once again paired up with their calves and released into the study pasture.

Supplement consumption rate (SCR) in confinement was the initial criterion used to classify individuals into presumed behavioural type (BT) groups (i.e. groups of cows possibly exhibiting different behavioural syndromes). Tests to measure SCR consisted of placing cows in individual feeding stalls and measuring their consumption rate of 908 g of cottonseed meal (36% CP), a protein supplement all animals were familiar with. Feeding stalls were 3 m long × 1.5 m wide and oriented so that cows entered and were held, immediately behind one another with metal slides separating them. Animals could see the cows in front of them and could look out the sides and see technicians and other cows. A stopwatch affixed to the side of the stall was used to measure the time it took an individually confined animal to consume the supplement offered. The timer was deployed as soon as the supplement was placed in the stall and stopped when the last piece of supplement was ingested. A few animals that refused to eat during classification trials were excluded from the study.

Each year we subjected all 80 cows in the herd to the classification test and selected the nine animals with fastest and slowest SCR (*n* = 18) which were classified into the *fast eater* (F) and *slow eater* (S) groups, respectively. Three cows (two in 2006 and one in 2007) lost their calf, and were therefore excluded from the final analysis which was conducted on data from the 33 remaining cows.

2.3. Validation of initial group classification

Consumption rates of cows classified into the F or S groups were timed every 2 weeks after the initial selection test to determine the repeatability of this behavioural trait through time. During subsequent tests, cows were again placed into individual feeding stalls and presented with 1.36 kg of supplement. Stalls had a stopwatch fixed to the side panel and the timer was started as soon as the supplement was offered and stopped when the last piece of supplement was ingested. If the entire amount of supplement was not consumed in 60 min, the refusal was weighed and total time was calculated by extrapolation assuming a constant consumption rate.

To determine whether classification into the F and S groups was associated with specific behavioural types (BTs), we conducted a blind classification of our entire data set (16 cows in 2006 plus 17 cows in 2007) using cluster analysis (McGarigal et al., 2000) to aggregate individuals into groups based on multivariate distances derived from a suite of predictors which included behavioural, physiological, and performance traits (see below).

Serum cortisol concentrations were measured in both years to infer potential differences in response to handling stress between cows segregated into distinct BT groups by the cluster analysis. Blood samples were collected via coccygeal venipuncture (Corvac, Sherwood Medical, St. Louis, MO, USA) from cows twice weekly after 35 days postpartum while confined in the individual feeding stalls. We sub-sampled blood collections from eight different days between 8 May and 19 July selecting days such that all trial animals had been bled at least twice previously. Following collection, samples were centrifuged at 2000 × *g* for 20 min at 4 °C. Serum was immediately harvested and frozen at −20 °C until assayed. Cortisol concentrations were quantified from serum samples by radioimmunoassay using components of a commercial kit (Siemens Healthcare Diagnostic, Los Angeles, CA, USA). Within and between assay coefficients of variation were less than 15%. Serum cortisol assays had been previously validated for ruminant serum by Kiyma et al. (2004).

2.4. Behavioural data

A suite of behaviours were measured on each animal (Table 1) which included: supplement consumption rate; pasture use patterns including the area covered and distance walked in a day, and daily time spent close to water and in each vegetation type; and feeding competition score (see below).
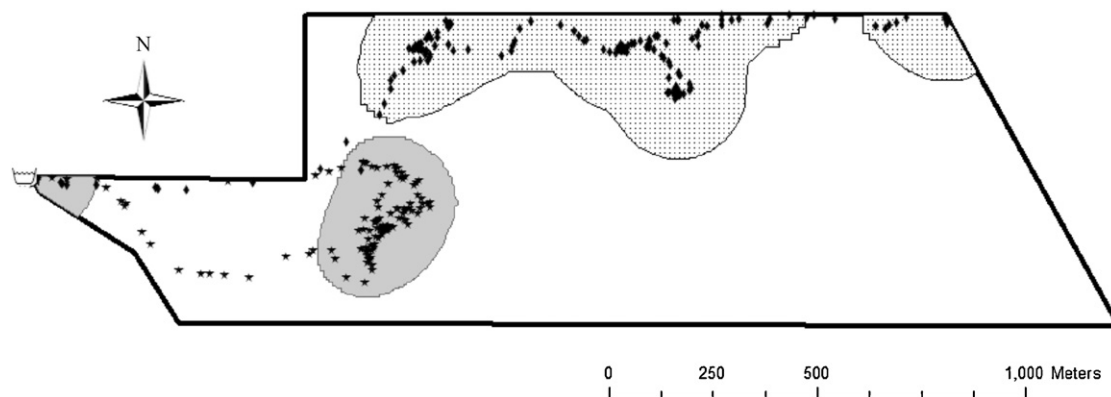
Fig. 1. Map of study pasture with 95% kernel volume density estimates of the daily grazing area covered by two behavioural types of cow (BT_1, light grey polygon and associated points and a BT_2, darker grey polygon and associated points).

Individual-based differences in landscape use patterns are an emerging focus of grazing behaviour research on rangelands (Searle et al., 2010) therefore, special emphasis was placed on assessing pasture exploration and use patterns of cows. Lotek® 2200 and 3300 GPS collars (Lotek Wireless, Newmarket, ON, Canada) were fitted on all cows in the study ($n = 36$; 18 each year) to monitor their pasture use patterns. Data collection began during the beginning of calving (3 March 2006 and 18 March 2007), and ended shortly before breeding (2 May 2006 and 11 May 2007). GPS receivers were set to store the position of each animal at 5 min intervals for 24 h and were deployed on Mondays and retrieved on Fridays. Data were downloaded and batteries charged over the weekend. GPS data collected on the cows were downloaded using the GPS host software (V2.062; Lotek Wireless Inc., Newmarket, ON, Canada) and then differentially corrected using Lotek's N4 software (V1.2138; Lotek Engineering Inc., Newmarket, ON, Canada) and using data from an Albuquerque base station of the National Geodetic Survey located approximately 150 km from our research site. Post processed location data were converted to UTM coordinates using Corpscon® (V6.0.1; US Army Corps of Engineers, Alexandria, VA, USA).

Pasture use variables were calculated using ArcGIS 9.2 (Environmental Systems Research Institute (ESRI), Redlands, CA, USA). First, a vegetation map (juniper vs. open grassland) was created by digitizing the juniper dominated areas on a digital aerial orthophoto image of the study pasture. A 50 m buffer polygon around the drinking water location was included in the map. Location of the watering point was collected using a handheld GPS unit (Thales Mobile Mapper, Santa Clara, CA, USA) with an accuracy of 3 m. Next, using Hawth's Analysis Tools for ArcGIS (v. 3.26; Beyer, 2004) we determined the number of times (5 min location points) each cow was positioned in a juniper stand and within the water buffer. Given that the study pasture consisted of two vegetation types with similar areas (approx. 45% juniper woodland and 55% open grassland), time spent in juniper woodland was used as a measure of vegetation type preference. Finally, using the home range tool within the Animal Movements v2.04 beta extension (Hooge and Eichenlaub, 1997) in ArcView 3.3 (Environmental Systems Research Institute (ESRI), Redlands, CA, USA), we determined the 95% fixed kernel as an estimate for the daily area covered by each cow. Kernel density probability functions provide a nonparametric

Table 1
List of variables measured on 33 young cows included in this study.

Category	Variable	Units
Initial classification criterion	Supplement consumption rate in confinement	g consumed /s
Physiology	Serum cortisol	ng/mL
Behaviour	Feeding competition	Index of displacement
	Distance travelled	m
	Area covered	ha
	Search pattern	m/ha
	Distance from water (mean)	m
	Distance travelled from water (max)	m
	Time spent at water	min
	Time spent in juniper woodland	%
Performance	Average body weight	kg
	Days from calving to body weight nadir	days
	Length of post partum anoestrus	days
	Calf body weight at birth and branding	kg
	Adjusted 205 day calf weaning weight	kg

estimation of the bivariate distribution of an animal's position in space within a defined confidence interval, usually 95% (Worton, 1989). The kernel density probability function uses a smoothing parameter, which in its simplest form is a fixed coefficient; Hooge and Eichenlaub's (1997) procedure in Animal Movements v2.04 sets this coefficient at $h = 0.8$, following Worton's (1989) recommendation. Distance measures (daily distance travelled, average and maximum distances from water) were derived using the Pythagorean Theorem in Microsoft Excel® (2003 Microsoft Corporation, USA). We also determined the distance travelled per area covered by dividing the daily distance travelled by the daily area covered as an indirect measure of sinuosity of an animal's trajectory.

Feeding competition contests were conducted in both years during a day when cows were not being tracked nor monitored for foraging behaviour/activity in the pasture. A displacement hierarchy was developed by placing all possible pairs of cows ($n = 147$) in a $36 \, m^2$ pen with three rubber feeding tubs, two empty and one containing crumbled pellet feed (12.5% CP) centrally placed 2 m apart. Two cows were turned into the arena at one time in a predefined random order with all possible combinations represented. The cow that was consistently able to displace her contest peer from a feeding tub or dominate the tub until the feed was depleted was declared the winner of the contest. The displacement hierarchy was formed by ranking a calculated index of displacement (index of displacement = number of matches won/number of matches won + number of matches lost) similar to Solano et al. (2004). In preparation for feeding competition contests, cows were placed in a pen with access to water but no food immediately following their evening grazing bout (20:00 h) the night prior to the matches. This was done to insure that cows were sufficiently motivated to compete for food during tests which were conducted between 07:00 and 14:00 h the following day.

2.5. Performance data

Because behavioural syndromes are thought to influence an individual's fitness (survival and reproductive success), a number of performance data were included in our analysis (Table 1). Cows were weighed weekly in both years and average weight and days to body weight (BW) nadir (lowest BW after calving) were determined. Calf BW was recorded within 3 d after birth and again at branding and weaning. Calf weaning BW was adjusted for a 205-d weaning BW and no adjustments were used for sex of calf or age of dam. In addition, length of post-partum anoestrus was determined for all cows in the study. Days to first oestrous were determined by analysing serum progesterone (two or more consecutive weekly samplings with serum progesterone concentrations ≥0.1 ng/mL) in blood samples collected via coccigeal venipuncture (Corvac, Sherwood Medical, St. Louis, MO, USA) weekly beginning approximately 35 d postpartum (Mulliniks et al., 2011).

2.6. Statistical analysis

A mixed-model approach with PROC MIXED (SAS version 9.1, SAS Inst., Cary, NC, USA) was used to determine the consistency of supplement consumption rate (SCR) classification through time. Each year was analysed separately and data were treated as a repeated measures (test date) model with SCR group as the main factor. The response variable measured was supplement consumption rate (g consumed/s). The Kenward–Rogers technique was used to partition the degrees of freedom, and an auto regressive covariance structure was used. Means were compared using the least square mean separation technique in SAS 9.1 (SAS Inst., Cary, NC, USA). An alpha level of $P \leq 0.05$ was used for all tests.

Cluster analysis was used to group all cows in the study based on multivariate distances derived from a suite of 14 predictors which comprised: (1) time to consume 908 g of feed (s); (2) average daily time spent in juniper woodland (%); (3) average daily distance travelled (m); (4) average daily distance from water (m); (5) maximum daily distance travelled from water (m); (6) average daily time spent within 50 m from water (min); (7) average area covered in one day (ha); (8) search pattern (ratio between daily distance travelled and area covered); (9) index of displacement in feeding competition trials; (10) blood cortisol concentration (ng/mL); (11) average body weight of cows (kg); (12) 205-day adjusted calf weaning weight (kg); (13) length of post partum anoestrus (days); and (14) days to BW nadir (days). CLUSTER and TREE procedures in SAS 9.1 (SAS Institute, Cary, NC, USA) were used to conduct these analyses. Average distance was used as the clustering technique using the PROC CLUSTER *method* = *average* option in SAS 9.1 (SAS Institute, Cary, NC).

A two sample *t*-test was used to determine if serum cortisol levels of groups classified by the cluster analysis procedure were detectably different ($P \leq 0.05$). We used PROC UNIVARIATE and PROC TTEST in SAS 9.1 (SAS Institute, Cary, NC, USA) to conduct this analysis after testing for violations of normality assumptions (Shapiro–Wilk test) and homogeneity of variances (folded *F*-test).

Discriminant function analysis (DA, McGarigal et al., 2000) is frequently used to classify animals into groups on the basis of multiple criteria such as the selection of diets (Hanley and Hanley, 1982; Ortega et al., 1997) or variation in behaviours (Bayley et al., 1997; Darden et al., 2003; Delgado, 2007). We used DA to: (a) determine if cows could be accurately discriminated into the groups identified by the cluster analysis using a linear discrimination function which included all 14 predictors used in the cluster analysis and (b) gain insights into the relative weight of predictors on the classification of cows into distinct BT groups. The second objective was achieved by analysing the weight of behaviour- and performance-related predictors (Table 1) in two separate DAs. Since consumption rate in confinement was used as the criterion to do the initial classification of groups, that variable was excluded from this analysis. To account for the possibility of having different number of animals in each group, we assumed proportional prior probability of group membership (McGarigal et al., 2000) using the *priors* = *proportional* option in SAS 9.1 (SAS
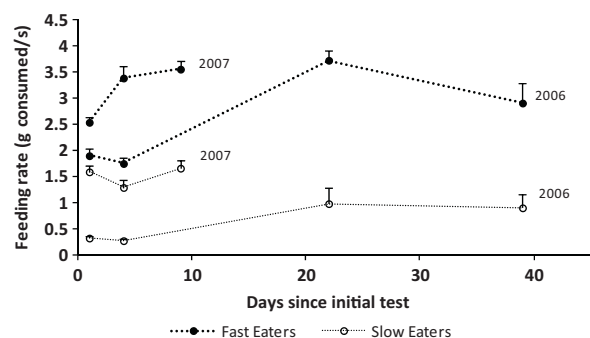
Fig. 2. Supplement consumption rates of *fast eaters* (F), and *slow eaters* (S). Consumption rate differences between groups within each year were statistically detectable ($P \leq 0.01$) on all dates. Bars indicate SEM.

Institute, Cary, NC, USA). The *covariance = test* option in SAS 9.1 (SAS Institute, Cary, NC, USA) was also used to test for equal variance–covariance structure across groups and to determine the appropriateness of the use of linear discriminant function. Wilk's Lambda was used in the MANOVA *F* tests to determine whether groups were detectably different ($P \leq 0.05$). When classification into detectably different groups was achieved, cross validation was conducted to determine the error rate of the discriminant function using the *crossvalidate* option in SAS 9.1 (SAS Institute, Cary, NC, USA).

Stepwise discriminant function analysis was conducted to determine the least set of predictors in the behaviour- and performance-related discriminant functions able to classify individuals correctly into BT groups. The alpha level to enter and retain variables in the stepwise procedure was $P = 0.10$. The DISCRIM and STEPDISC procedures in SAS 9.1 (SAS Institute, Cary, NC, USA) were used to perform statistical analyses.

Finally, relationships among behaviours and between behavioural and either physiological or fitness-related variables were examined using linear correlation analysis to study all one-way associations between response variables measured on all cows. The CORR procedure in SAS 9.1 (SAS Inst., Cary, NC, USA) was used to calculate Pearson correlation coefficients.

3. Results

Initial classification of cows resulted in the selection of two groups of animals with contrasting supplement consumption rates (g consumed/s) both in 2006 (mean ± SE: 1.90 ± 0.14 vs. 0.32 ± 0.03 g/s; $P < 0.01$) and 2007 (2.54 ± 0.11 vs. 1.59 ± 0.13 g/s; $P < 0.01$) (Fig. 2). The herd SCR mean ± SE and range for 2006 and 2007 were 0.84 ± 0.07 g/s; 0.2–2.1 g/s and 2.41 ± 0.17 g/s; 0.8–4.4 g/s, respectively. Statistical differences between groups persisted through successive tests (four in 2006 and three in 2007) conducted over 39 and 9 days in the first and second years of the study, respectively (Fig. 2). In 2007, no cows with low consumption rates similar to those recorded in 2006 were found. Cows classified into the S group in 2007 exhibited consumption rates that were similar to those of cows classified into the F group in 2006 (Fig. 2).

Cluster analysis discriminated three groups of individuals: (a) a cluster of 25 cows including all individuals placed in the F group in 2006 and 2007 in addition to cows classified as *slow eaters* in 2007 (cluster 1 in Fig. 3); (b) a cluster of 3 cows that had been classified as *slow eaters* in 2006 (cluster 2 in Fig. 3); and (c) a cluster of 5 cows which had also been placed in the S group in 2006 (cluster 3 in Fig. 3). No discrimination of individuals into discrete groups was possible in 2007; all cows in this year were classified in a single cluster with animals belonging to the F group. Interestingly, some of the closest associations on the cluster analysis dendrogram occurred between pairs of F (2006) and S (2007) individuals (e.g., 77_F_06 and 05_S_07; 04_S_07 and 95_F_06; 64_F_06 and 27_S_07 in Fig. 3). Three exploratory DA iterations were conducted using the same 14 predictors included in the cluster analysis to determine the most appropriate group affiliation of cows classified into the intermediate group (cluster 2 in Fig. 3). These analyses indicated that the best classification (lowest overall error rate in the cross-validation procedure) was achieved by assuming two groups (cluster 1 vs. clusters 2 and 3). Therefore, subsequent analyses considered the 25 cows segregated into cluster 1, and the 8 cows segregated into clusters 2 and 3 as belonging to two distinct behavioural types; BT_1 and BT_2, respectively. The first group included cows initially classified as *fast eaters* (F) in 2006 and all cows included in the study in 2007, whereas the second group included all cows classified as *slow eaters* (S) in 2006.

Mean serum cortisol levels appeared to provide additional support for the cluster classification described above. Cows classified into the BT_1 category exhibited significantly higher levels ($t = 3.20$; $P < 0.01$) of serum cortisol (8.8 ± 0.88 ng/mL) than their BT_2 counterparts (5.5 ± 0.51 ng/mL). Although no formal fear response tests were conducted, animals in the BT_1 group consistently exhibited a higher degree of nervousness when approached by a human and showed an overall bolder disposition than cows in the BT_2 group.

Feeding competition displacement indices were almost identical for both groups (BT_1: 0.50 ± 0.04 vs. BT_2: 0.49 ± 0.09) and were therefore excluded from the DA which assessed the influence of measured behaviour on group membership of cows. The suite of seven spatial behaviours included in the classification function was able to discriminate BT_1 and BT_2 cows into statistically different groups ($F = 24.5$; $P < 0.01$; Table 2) with an 18% overall cross-classification error rate (four BT_1 and two BT_2 individuals were misclassified). The spatial search pattern of cows was the variable that most heavily weighed on the classification of individuals. Cows classified as exhibiting BT_2 tended to have a more concentrated search pattern than their BT_1 counterparts that tended to cover larger areas and exhibit a less tortuous trajectory (Table 2). The area of the pasture covered in a day was the second most influential classification variable; on average, BT_1 cows tended to cover four hectares more than their BT_2 counterparts on any given day. Time spent at water, and distance travelled from water were the third and fourth most influential classification variables (Table 2). Cows exhibiting BT_2 spent more than twice as much time close to the water drinker than their BT_1 counterparts and did not travel as far from water as
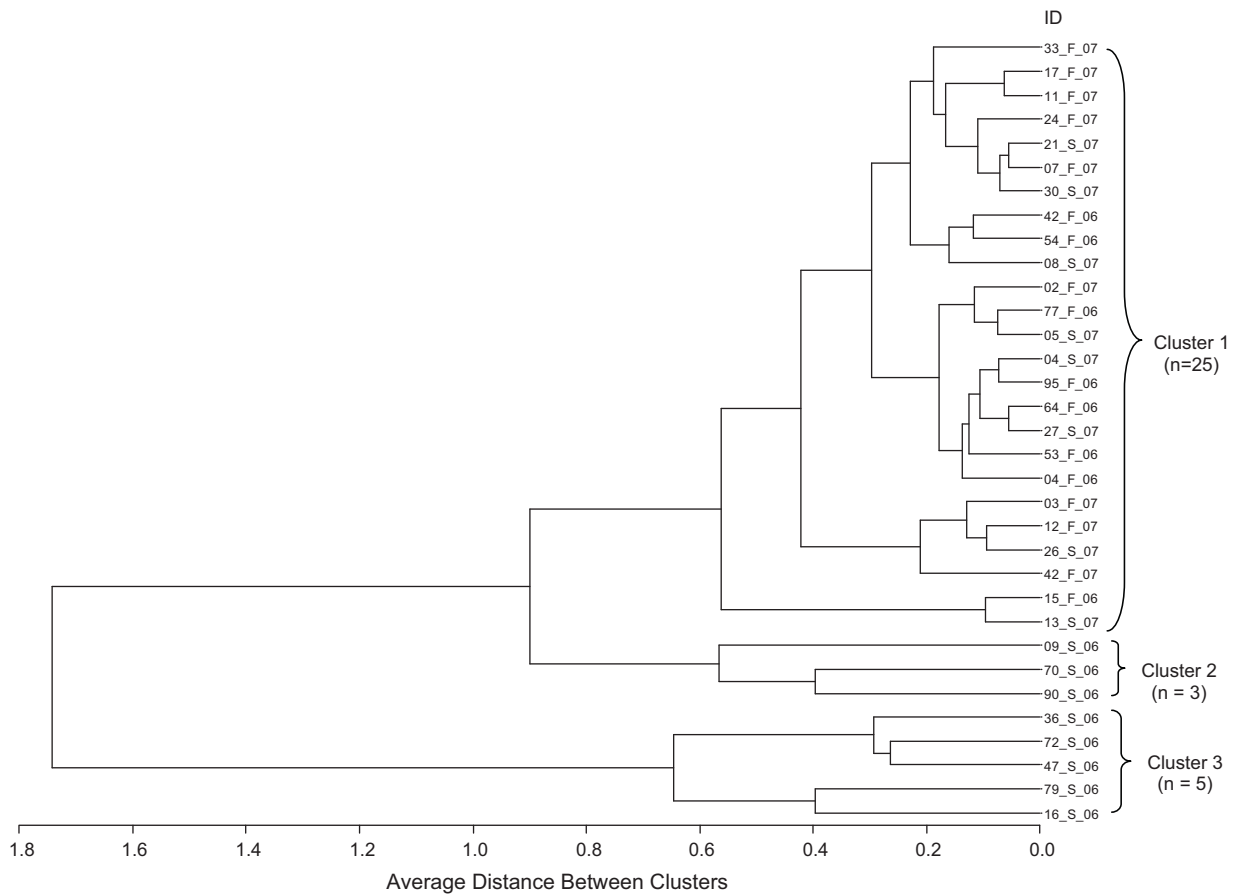
Fig. 3. Cluster analysis dendrogram of 33 cows classified on the basis of 14 predictors. Individual animal identification code indicates the last two numbers of its ear tag, whether the individual had been classified as a *fast eater* (F) or *slow eater* (S) in initial classification trials, and whether the individual was monitored in 2006 (06) or 2007 (07).

did BT_1 cows. Spatial search pattern, distance from water, and time spent close to the water drinker were the three variables selected by the stepwise procedure as the minimum set of predictors able to discriminate BT_1 and BT_2 cows into significantly different groups (Table 2).

The suite of four performance-related predictors used in the second explanatory DA was able to discriminate BT_1 and BT_2 cows into statistically different groups ($F = 6.85$; $P < 0.01$; Table 3) with a 21% cross-classification error rate (three BT_1 and four BT_2 individuals were misclassified). The two measures of individual performance, days to reach BW nadir and BW, were the most influential classification variables and were also the only two predictors selected by the discriminant stepwise procedure (Table 3). After

Table 2

Discriminant function analysis results including all spatial behaviour predictors. A priori group membership of cows in the BT_1 vs. BT_2 categories was determined using cluster analysis (Fig. 3).

Response variable	Standardized coefficient	Mean ± SE	
		BT_1 ($n = 25$)	BT_2 ($n = 8$)
Distance travelled (m)	−4.19	5322 ± 127.2	5195 ± 207.6
Area covered (ha)	5.32	21 ± 0.6	17 ± 1.5
* **Spatial search pattern (m/ha)**[a]	**7.76**	**264 ± 8.9**	**314 ± 26.1**
* **Distance from water (mean) (m)**	**4.32**	**886 ± 16.2**	**835 ± 42.9**
Distance travelled from water (max) (m)	−0.89	1376 ± 22.7	1309 ± 36.9
* **Time spent at water (min)**	**4.52**	**73 ± 10.1**	**172 ± 15.5**
Time spent in juniper woodland (%)	−1.48	23 ± 3.0	39 ± 8.2
Wilks' Lambda		0.56	
F		24.51	
P		< 0.01	

[a] Asterisks and bold type identify response variables that were selected in the stepwise procedure.

Table 3
Discriminant function analysis results including all cow performance measures. A priori group membership of cows in the BT_1 vs. BT_2 categories was determined using cluster analysis (Fig. 3).

Response variable	Standardized coefficient	Mean ± SE	
		BT_1 ($n = 25$)	BT_2 ($n = 8$)
* **Body weight (kg)[a]**	**−1.34**	**433.6 ± 6.6**	**394.4 ± 9.9**
* **Days to body weight nadir (days)**	**1.53**	**43.7 ± 2.9**	**69.0 ± 6.4**
Length of post partum anoestrus (days)	0.76	71.5 ± 4.3	89.4 ± 6.3
Adjusted 205 day calf weaning weight (kg)	−0.17	199.8 ± 6.2	179.0 ± 7.0
Wilks' Lambda		0.50	
F		6.91	
P		< 0.01	

[a] Asterisks and bold font indicate response variables that were selected in the stepwise procedure.

calving, BT_1 cows began gaining weight 25 days sooner and were on average 39 kg heavier than their BT_2 counterparts. Although, reproduction-related variables weighed less heavily on the classification of cows and were not selected in the stepwise procedure, on average, BT_1 cows tended to wean heavier calves and began cycling sooner after calving than their BT_2 counterparts (Table 3).

Correlation analysis showed significant linear associations between supplement consumption rate in the stalls and all response variables except two: displacement index; and length of postpartum anoestrus (Table 4). These relationships largely confirmed trends observed in the validation tests and discriminant analyses described above but provided new insights into: (a) vegetation use patterns not captured by previous analyses and (b) relationships between spatial behaviours, social behaviours, and animal performance (fitness measures). Increasing time spent in juniper woodland was associated with slower supplement consumption rates in stalls, more time at water, smaller areas covered in a day, and lighter weaning weights of calves (Table 4). Collectively, these correlations suggest that BT_2 cows may have shown higher preference for juniper woodlands. These data also suggest that besides showing contrasting spatial behaviours (as indicated by the discriminant analyses) animals with contrasting BTs may also exhibit different plant community selection patterns. Distance travelled, was not associated with any of the cow performance traits measured. Conversely, all other spatial behaviour variables showed significant relationships with one or more performance responses (Table 4). Calf weaning weights were significantly associated with area covered (+), distance travelled from water (+), spatial search pattern (−), time at water (−), and time in woodland (−) confirming the tendency of BT_1 cows to wean heavier calves observed in the discriminant analyses reported above. Displacement index (derived from the feeding competition tests) tended ($P \leq 0.10$) to be associated with distance travelled (+) and body weight (+).

4. Discussion

We were able to select cows with consistently different supplement consumption rates into two groups that also exhibited distinct rangeland use patterns. Cattle that consumed supplement rapidly in confinement (BT_1) exhibited higher serum cortisol levels, tended to cover larger areas of rangeland pasture and to exhibit less concentrated search patterns, and showed a tendency to spend less time close to water (presumably loafing) than their BT_2 counterparts that consumed supplements at very slow rates. The suite of correlated feeding-related behaviours measured multiple times in two contrasting contexts (stalls and rangeland pasture) suggest that the F and S supplement feeding rates were associated with distinct behavioural types (Luttbeg and Sih, 2010). Furthermore, behavioural syndromes of each BT were associated with differences in animal performance which are of both economical and ecological consequence to commercial cow-calf operations.

Koolhaas et al. (1999) studied a specific kind of behavioural type categories which they referred to as animal stress coping styles. These authors identified two general behavioural types that occur across a broad array of taxa which they termed *proactive* vs. *reactive* stress coping styles. According to these authors, the behaviour of proactive individuals includes short attack latencies, active avoidance, defensive aggression, aggressive territorial control, and forming rigid routines. Reactive individuals, on the other hand, tend to have a more conservative withdrawal response, adapt quicker, and respond with immobility when confronted with danger. Although we did not measure a number of the temperament traits used to describe stress coping styles (Koolhaas et al., 1999, 2007), our BT_1 and BT_2 behavioural type groups appeared to share a number of the proactive (BT_1) and reactive (BT_2) coping style characteristics.

Serum cortisol concentrations were positively correlated with supplement consumption rate and were detectably higher in cows classified into the BT_1 group. A number of beef-cattle temperament studies have reported a positive relationship between blood cortisol levels and measures of excitability and boldness in beef cattle (Curley et al., 2006; Petherick et al., 2009b). During supplement feeding tests and when subjected to GPS collar placement and removal in the squeeze chute or stalls, cows in the BT_1 group consistently exhibited a higher degree of nervousness when approached by a human and showed an overall bolder disposition than cows in the BT_2 group.

Despite differences in serum cortisol levels between BT_1 and BT_2 cows, the overall values observed in this study were slightly lower than those reported in *Bos taurus*

Table 4

Pearson correlation coefficients for all pair-wise associations between variables measured on 33 young rangeland-raised cows. Shaded cells indicate significant associations between variables at $P \leq 0.05$ (*) or $P \leq 0.10$ (†).[a]

		Serum cortisol	Distance travelled	Area covered	Spatial search pattern	Distance travelled from water		Time at water	Time in woodl.	DI[c]	Body weight	Days to BWN	Calf wean. weight	Post partum anoestrus
						Mean	Max							
SCR[b]		0.35*	0.36*	0.50*	−0.29†	0.43*	0.51 *	−0.73 *	−0.45*	0.13	−0.53*	0.49*	−0.43*	−0.07
Serum cortisol			0.20	0.10	−0.02	0.24	0.44*	−0.40*	−0.22	−0.02	0.39*	−0.53*	0.06	−0.32†
Distance travelled				0.11	0.41*	0.31	0.59*	−0.31†	−0.18	0.32†	0.21	−0.04	0.23	0.25
Area covered					−0.83*	0.35*	0.26	−0.43*	−0.31	−0.11	0.18	−0.48*	0.43*	0.01
Spatial search pattern						−0.20	0.02	0.27	0.16	0.21	−0.11	0.44*	−0.27	0.20
Distance travelled from water	Mean						−0.60*	−0.64*	0.25	0.15	0.28	−0.41*	0.30†	−0.09
	Max										0.35*	−0.38*	0.36*	0.05
Time at water									0.40*	0.08	−0.39*	0.54*	−0.60*	0.21
Time in woodland										−0.19	−0.15	0.28	−0.44*	−0.11
DI[b]											0.29†	0.14	0.01	0.12
Body weight												−0.23	0.18	−0.21
Days to BWN													−0.51*	0.24
Calf weaning weight														−0.05

[a] P values were not adjusted for multiple comparisons therefore statistical significance must be interpreted with caution.

[b] Supplement consumption rate in confinement.

[c] Displacement index measured in feeding competition trials.

(Bristow and Holmes, 2007) or *Bos indicus* cows (Solano et al., 2004), and in dairy heifers (Adeyemo and Heath, 1982), and much lower than values reported by Curley et al. (2006) in feedlot steers. The CRLRC cow herd may be better adapted to stressful situations due to frequent handling, and could therefore have lower than average HPA axis reactivity releasing lower than expected levels of cortisol in situations of confinement. Alternatively, most of our blood samples may have been collected after peak concentrations of serum cortisol occurred. Lay et al. (1996) reported that plasma cortisol concentrations peaked 15–45 min after an injection of adrenocorticotropic (ACTH) hormone in pregnant *Bos indicus* cows, and plasma cortisol concentrations took longer than 20 min after restraint to peak in young calves (Lay et al., 1992). Our collections were made within 40–60 min of gathering cows into the holding pens and sorting calves, thus cortisol concentration was probably decreasing at the time of sampling.

Consistency of individual behaviours through time have been identified in beef cattle (Curley et al., 2006; Nkrumah et al., 2006; Petherick et al., 2009a), dairy cattle (Muller and Schrader, 2005a,b; Van Reenen et al., 2004) and goats (Lyons et al., 1988) and have been ascribed to temperaments, animal personalities, or degrees of fearfulness. Studies that investigated correlations among behaviours across different contexts in cattle have typically been conducted with young animals exposed to fear-eliciting stimuli (Grignard et al., 2001; Van Reenen et al., 2004). None of these studies, however, included pasture foraging contexts like those examined in our study. Individual differences in pasture use patterns of beef cattle on rangelands, on the other hand, have been observed repeatedly (Bailey et al., 2006) and have been explained in terms of social cohesiveness (Roath and Krueger, 1982), social learning (Howery et al., 1996) or as the result of breed-related differential selection pressures (Peinetti et al., 2011; VanWagoner et al., 2006). Although Roath and Krueger (1982) and Bailey et al. (2006) did not classify animals into behavioural types, they observed a somewhat bimodal frequency distribution of spatial behaviours; some cows in the herds they monitored consistently travelled farther from water (streams) than others which were more prone to remain in flat terrain close to streams, a result which is somewhat analogous to the behavioural type differences observed in our study.

Although frequency distribution of animal behavioural types in natural populations is often assumed to be bimodal, individuals can often be sorted along continuums of personality, temperament, or stress coping styles (Koolhaas et al., 1999; Réale et al., 2007). This is particularly true of domestic livestock where artificial selection pressure usually results in culling of individuals with less adapted behavioural types. For example, Ruis et al. (2000) were able to separate two groups of gilts with either proactive- or reactive-like personalities by selecting individuals with extreme first backtest scores. We followed a somewhat similar approach selecting young cows with fastest or slowest supplement consumption rates but the degree of behavioural variation was different in the 2006 vs. the 2007 group. The majority of 2- and 3-yr-old cows in the CRLRC herd appeared to exhibit a BT_1-like

behavioural type which hindered our ability to identify BT_2 individuals in the second year of the study. Because all non-pregnant non-lactating cows at CRLRC are culled each autumn regardless of age and prior reproductive record, it is possible that individuals with extreme BT_2 traits (and expected poorer reproductive performance) were being selected against and were therefore scantly represented in the herd. Cows that exhibited BT_1, on the other hand, were apparently better suited to the rangeland environment of our study site during the two years of this experiment.

The index of displacement derived from feeding contests did not influence the discrimination of individuals and was not correlated with supplement consumption rate or serum cortisol concentrations. Because we conducted dyad contests rather than assess group interactions we were unable to determine true group dominance in this herd (Beilharz and Zeeb, 1982). Langbein and Puppe (2004) developed dominance hierarchies at both the dyadic and group level and concluded that a hierarchy is only reasonable when both levels are combined. Nonetheless, trends for positive correlations ($P \leq 0.10$) between DI and both distance travelled and body weight suggests that resource acquisition patterns and animal performance may be related, albeit weakly, with social behaviours of cows in this herd.

Variation in rangeland use patterns of cows in our study was significantly associated with animal performance. These findings differ from those reported by VanWagoner et al. (2006) but are in apparent agreement with results of a meta-analysis conducted by Smith and Blumstein (2008) that included 37 studies addressing the fitness consequences of animal personality. This analysis collectively showed that exploration had a positive effect on an individual's survival, and that boldness was positively associated to an individual's reproductive success. BT_1 cows in our study tended to cover larger areas, and to spend less time loafing close to water, they tended to begin gaining weight sooner after calving, were heavier, tended to wean heavier calves, and to have a shorter post-partum anoestrus period than their BT_2 counterparts. Pasture exploration patterns of BT_1 cows may have afforded them better access to heterogeneously distributed forage resources in this semiarid rangeland environment. This could have resulted in better productive and reproductive performance values observed. Interestingly, distance travelled which is a frequent indicator of spatial behaviour used in livestock GPS studies (Bailey et al., 2010; Ganskopp and Bohnert, 2006; Schauer et al., 2005) was not correlated with any of the animal performance variables measured.

The relationships between rangeland use patterns and animal performance found in this study appear to contradict results of studies conducted in confined feeding contexts (feedlots). In such environments, cattle with bolder and more excitable temperaments (comparable to our BT_1 group) exhibit lower weight gains (Burrow and Dillon, 1997; Nkrumah et al., 2007b; Voisinet et al., 1997b), produce tougher meat (Voisinet et al., 1997a), yield increased amounts of bruise trim due to injuries acquired during transportation (Fordyce et al., 1988b), and exhibit greater incidence of dark cutting (Scanga et al., 1998). Cattle at the CRLRC are selected for ease of

handling and therefore exhibit fairly mild temperaments. No animals with extremely aggressive or wild temperaments such as those described by Fordyce et al. (1988a) were present in either group in this study. Therefore, excitability differences between animals exhibiting BT_1 vs. BT_2 may have represented different degrees of a calm temperament (Voisinet et al., 1997b). Alternatively, BT_1 cattle may exhibit higher fitness levels in a free-ranging context where restlessness and an apparent higher drive to explore the landscape may be advantageous. This behavioural syndrome, however, could cause cattle to underperform in a feedlot environment where excitability may lead to higher levels of stress and lower weight gains. The opposite could be true of BT_2 cows.

Several authors have advocated culling individuals with undesirable rangeland use patterns as a means of promoting more uniform grazing of rangeland pastures (Bailey et al., 2006; Howery et al., 1996). We argue that pasture use behaviours must be studied within the theoretical framework of behavioural syndromes to determine behavioural constraints limiting an animal's ability to adapt to changes in its context (Bell, 2007b). Insights provided by this approach could guide selection decisions, particularly if behavioural syndromes are heritable and set constraints on the industry's ability to optimize animal fitness levels simultaneously for both rangeland and feedlot environments.

5. Conclusions

We were able to segregate young rangeland cows into statistically different groups on the basis of a suite of correlated behaviours. Animals that consumed supplements at faster rates in confinement (BT_1), exhibited higher serum cortisol levels, tended to cover larger rangeland areas in a given day, exhibited a less tortuous trajectory, tended to spend less time at water and to travel farther from water than their BT_2 counterparts. Cows exhibiting BT_1 appeared to perform better (in terms of weight gains and reproductive efficiency) and are possibly better adapted to this rangeland environment. Further research is needed to determine whether the offspring of the apparently more adapted behavioural type is able to outperform BT_2 peers in both rangeland and feedlot environments.

References

Adeyemo, O., Heath, E., 1982. Social behaviour and adrenal cortical activity in heifers. Appl. Anim. Ethol. 8, 99–108.

Bailey, D.W., VanWagoner, H.C., Weinmeister, R., 2006. Individual animal selection has the potential to improve uniformity of grazing on Foothill Rangeland. Rangeland Ecol. Manage. 59, 351–358.

Bailey, D.W., Witmore, B.K., Tolleson, D., Thomas, M.G., Walker, J.W., 2010. Effect of previous experience on grazing patterns and diet selection of brangus cows in the Chihuahuan Desert. Rangeland Ecol. Manage. 63, 223–232 (electronic resource).

Bayley, M., Baartup, E., Bjerregaard, P., 1997. Woodhouse locomotor behavior in the assessment of clean and contaminated field sites. Environ. Toxicol. Chem. 16, 2309–2314.

Beilharz, R.G., Zeeb, K., 1982. Social dominance in dairy cattle. Appl. Anim. Ethol. 8, 79–97.

Bell, A.M., 2007a. Evolutionary biology: animal personalities. Nature 447, 539–540.

Bell, A.M., 2007b. Future directions in behavioural syndromes research. Proc. R. Soc. Biol. Sci. Ser. B 274, 755–761.

Benhajali, H., Boivin, X., Sapa, J., Pellegrini, P., Boulesteix, P., Lajudie, P., Phocas, F., 2010. Assessment of different on-farm measures of beef cattle temperament for use in genetic evaluation. J. Anim. Sci. 88, 3529–3537.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS [computer program]. Available at: http://www.spatialecology.com/htools. Accessed 20 April 2012.

Bristow, D.J., Holmes, D.S., 2007. Cortisol levels and anxiety-related behaviors in cattle. Physiol. Behav. 90, 626–628.

Burrow, H.M., Dillon, R.D., 1997. Relationships between temperament and growth in a feedlot and commercial carcass traits of Bos indicus crossbreds. Aust. J. Exp. Agric. 37, 407–411.

Core, S., Widowski, T., Mason, G., Miller, S., 2009. Eye white percentage as a predictor of temperament in beef cattle. J. Anim. Sci. 87, 2168–2174.

Curley Jr., K.O., Neuendorff, D.A., Lewis, A.W., Rouquette Jr., F.M., Randel, R.D., Welsh Jr., T.H., 2011. The effectiveness of vasopressin as an ACTH secretagogue in cattle differs with temperament. Physiol. Behav. 101, 699–704.

Curley, K.O., Paschal, J.C., Welsh, T.H., Randel, R.D., 2006. Technical note: exit velocity as a measure of cattle temperament is repeatable and associated with serum concentration of cortisol in Brahman bulls. J. Anim. Sci. 84, 3100–3103.

Darden, S.K., Dabelsteen, T., Pedersen, S.B., 2003. A potential tool for swift fox (*Vulpes velox*) conservation: individuality of long-range barking sequences. J. Mammal. 84, 1417–1427.

Delgado Jr., R.A., 2007. Geographic variation in the long calls og male orangutans (*Pongo* spp.). Ethol. 113, 487–498.

Fordyce, G., Dodt, R.M., Wythes, J.R., 1988a. Cattle temperaments in extensive beef herds in northern Queensland. 1. Factors affecting temperament. Aust. J. Exp. Agric. 28, 683–687.

Fordyce, G., Wythes, J.R., Shorthose, W.R., Underwood, D.W., Shepherd, R.K., 1988b. Cattle temperaments in extensive beef herds in northern Queensland. 2. Effect of temperament on carcass and meat quality. Aust. J. Exp. Agric. 28, 689–693.

Ganskopp, D., Bohnert, D., 2006. Do pasture-scale nutritional patterns affect cattle distribution on rangelands? Rangeland Ecol. Manage. 59, 189–196.

Gosling, S.D., 2001. From mice to men: What can we learn about personality from animal research? Psychol. Bull. 127, 45–86.

Grandin, T., Deesing, M.J., Struthers, J.J., Swinker, A.M., 1995. Cattle with hair whorl patterns above the eyes are more behaviorally agitated during restraint. Appl. Anim. Behav. Sci. 46, 117–123.

Grignard, L., Boivin, X., Boissy, A., Le Neindre, P., 2001. Do beef cattle react consistently to different handling situations? Appl. Anim. Behav. Sci. 71, 263–276.

Gutiérrez-Gil, B., Ball, N., Burton, D., Haskell, M., Williams, J.L., Wiener, P., 2008. Identification of quantitative trait loci affecting cattle temperament. J. Hered. 99, 629–638.

Hall, N.L., Buchanan, D.S., Anderson, V.L., Ilse, B.R., Carlin, K.R., Berg, E.P., 2011. Working chute behavior of feedlot cattle can be an indication of cattle temperament and beef carcass composition and quality. Meat Sci. 89, 52–57.

Hanley, T.A., Hanley, K.A., 1982. Food resource partitioning by sympatric ungulates on Great Basin Rangeland. J. Range Manage. 35, 152–158.

Hooge, P.N., Eichenlaub, B., 1997. In: Alaska Science Center-Biological Science Office, U.S.G. Survey (Ed.), Animal Movement Extension to Arcview. Version 1.1. Anchorage, AK.

Howery, L.D., Provenza, F.D., Banner, R.E., Scott, C.B., 1996. Differences in home range and habitat use among individuals in a cattle herd. Appl. Anim. Behav. Sci. 49, 305–320.

Kiyma, Z., Alexander, B.M., Van Kirk, E.A., Murdoch, W.J., Hallford, D.M., Moss, G.E., 2004. Effects of feed restriction on reproductive and metabolic hormones in ewes. J. Anim. Sci. 82, 2548–2557.

Koolhaas, J.M., de Boer, S.F., Buwalda, B., van Reenen, K., 2007. Individual variation in coping with stress: a multidimensional approach of ultimate and proximate mechanisms. Brain Behav. Evol. 70, 218–226.

Koolhaas, J.M., de Boer, S.F., Coppens, C.M., Buwalda, B., 2010. Neuroendocrinology of coping styles: towards understanding the biology of individual variation. Front. Neuroendocrinol. 31, 307–321.

Koolhaas, J.M., Korte, S.M., DeBoer, S.F., Van Der Vegt, B.J., Van Reenen, G.G., Hopster, H., De Jong, I.C., Ruis, M.A.W., Blokhuis, H.J., 1999. Coping styles in animals: current status in behavior and stress physiology. Neurosci. Biobehav. Rev. 23, 925–935.

Langbein, J., Puppe, B., 2004. Analysing dominance relationships by sociometric methods—a plea for a more standardised and precise approach in farm animals. Appl. Anim. Behav. Sci. 87, 293–315.

Lay, D.C., Friend, T.H., Randel, R.D., Bowers, C.L., Grissom, K.K., Jenkins, O.C., 1992. Behavioral and physiological effects of freeze or hot-iron branding on crossbred cattle. J. Anim. Sci. 70, 330–336.

Lay, D.C., Friend, T.H., Randel, R.D., Jenkins, O.C., Neuendorff, D.A., Kapp, G.M., Bushong, D.M., 1996. Adrenocorticotropic hormone dose response and some physiological effects of transportation on pregnant Brahman cattle. J. Anim. Sci. 74, 1806–1811.

Luttbeg, B., Sih, A., 2010. Risk, resources and state-dependent adaptive behavioural syndromes. Philos. Trans. R. Soc. Lond. B: Biol. Sci. 365, 3977–3990.

Lyons, D.M., Price, E.O., Moberg, G.P., 1988. Individual differences in temperament of domestic dairy goats: constancy and change. Anim. Behav. 36, 1323–1333.

McGarigal, K., Cushman, S., Stafford, S., 2000. Multivariate Statistics for Wildlife and Ecology Research. Springer, New York.

Muller, R., Schrader, L., 2005a. Behavioural consistency during social separation and personality. Behaviour 142, 1289–1306.

Muller, R., Schrader, L., 2005b. Individual consistency of dairy cows' activity in their home pen. J. Dairy Sci. 88, 171–175.

Mulliniks, J.T., Kemp, M.E., Cox, S.H., Hawkins, D.E., Cibils, A.F., VanLeeuwen, D.M., Petersen, M.K., 2011. The effect of increasing amount of glucogenic precursors on reproductive performance in young postpartum range cows. J. Anim. Sci., http://dx.doi.org/10.2527/jas.2010-3198.

Nkrumah, J.D., Crews, D.H., Basarab, J.A., Price, M.A., Okine, E.K., Wang, Z., Li, C., Moore, S.S., 2007a. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. J. Anim. Sci. 85, 2382–2390.

Nkrumah, J.D., Crews Jr., D.H., Basarab, J.A., Price, M.A., Okine, E.K., Wang, Z., Li, C., Moore, S.S., 2007b. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. J. Anim. Sci. 85, 2382–2390.

Nkrumah, J.D., Okine, E.K., Mathison, G.W., Schmid, K., Li, C., Basarab, J.A., Price, M.A., Wang, Z., Moore, S.S., 2006. Relationships of feedlot feed efficiency, performance, and feeding behavior with metabolic rate, methane production, and energy partitioning in beef cattle. J. Anim. Sci. 84, 145–153.

Olmos, G., Turner, S.P., 2008. The relationships between temperament during routine handling tasks, weight gain and facial hair whorl position in frequently handled beef cattle. Appl. Anim. Behav. Sci. 115, 25–36.

Ortega, I.M., Soltero-Gadea, S., Bryant, F.C., Drawe, D.L., 1997. Evaluating grazing strategies for cattle: deer and cattle food partitioning. J. Range Manage. 50, 622–630.

Peinetti, H.R., Fredrickson, E.L., Peters, D.P.C., Cibils, A.F., Roacho-Estrada, J.O., Laliberte, A.S., 2011. Foraging dynamics of heritage versus recently introduced herbivores on desert landscapes of the American Southwest. Ecosphere 2, art57.

Petherick, J.C., Doogan, V.J., Holroyd, R.G., Olsson, P., Venus, B.K., 2009a. Quality of handling and holding yard environment, and beef cattle temperament: 1. Relationships with flight speed and fear of humans. Appl. Anim. Behav. Sci. 120, 18–27.

Petherick, J.C., Doogan, V.J., Venus, B.K., Holroyd, R.G., Olsson, P., 2009b. Quality of handling and holding yard environment, and beef cattle temperament: 2. Consequences for stress and productivity. Appl. Anim. Behav. Sci. 120, 28–38.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. 82, 291–318.

Roath, L.R., Krueger, W.C., 1982. Cattle grazing and behavior on a forested range. J. Range Manage. 35, 332–338.

Ruis, M.A.W., te Brake, J.H.A., van de Burgwal, J.A., de Jong, I.C., Blokhuis, H.J., Koolhaas, J.M., 2000. Personalities in female domesticated pigs: behavioural and physiological indications. Appl. Anim. Behav. Sci. 66, 31–47.

Scanga, J.A., Belk, K.E., Tatum, J.D., Grandin, T., Smith, G.C., 1998. Factors contributing to the incidence of dark cutting beef. J. Anim. Sci. 76, 2040–2047.

Schauer, C.S., Bohnert, D.W., Ganskopp, D.C., Richards, C.J., Falck, S.J., 2005. Influence of protein supplementation frequency on cows consuming low-quality forage: performance, grazing behavior, and variation in supplement intake. J. Anim. Sci. 83, 1715–1725.

Schuehle Pfeiffer, C.E., King, D.A., Lucia, L.M., Cabrera-Diaz, E., Acuff, G.R., Randel, R.D., Welsh Jr., T.H., Oliphint, R.A., Curley Jr., K.O., Vann, R.C., Savell, J.W., 2009. Influence of transportation stress and animal temperament on fecal shedding of Escherichia coli O157:H7 in feedlot cattle. Meat Sci. 81, 300–306.

Searle, K.R., Hunt, L.P., Gordon, I.J., 2010. Individualistic herds: Individual variation in herbivore foraging behavior and application to rangeland management. Appl. Anim. Behav. Sci. 122, 1–12.

Sih, A., Bell, A.M., Johnson, C.J., Ziembra, R.E., 2004a. Behavioral syndromes: an integrative overview. Q. Rev. Biol. 79, 242–277.

Sih, A., Bell, A., Johnson, C., 2004b. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol. Evol. 19, 372–378.

Sih, A., Bell, A.M., 2008. Insights for behavioral ecology from behavioral syndromes. Advances in the Study of Behavior, vol. 38. Elsevier Academic Press Inc, San Diego, pp. 227–281.

Smith, B.R., Blumstein, D.T., 2008. Fitness consequences of personality: a meta-analysis. Behav. Ecol. 19, 448–455.

Solano, J., Galindo, F., Orihuela, A., Galina, C.S., 2004. The effect of social rank on the physiological response during repeated stressful handling in Zebu cattle. Physiol. Behav. 82, 679–683.

Stamps, J., Groothuis, T.G.G., 2010. The development of animal personality: relevance, concepts and perspectives. Biol. Rev. 85, 301–325.

Van Reenen, C.G., Engel, B., Ruis-Heutinck, L.F.M., Van der Werf, J.T.N., Buist, W.G., Jones, R.B., Blokhuis, H.J., 2004. Behaviour reactivity of heifer calves in potentially alarming test situations: a multivariate and correlational analysis. Appl. Anim. Behav. Sci. 85, 11–30.

VanWagoner, H.C., Bailey, D.W., Kress, D.D., Anderson, D.C., Davis, K.C., 2006. Differences among beef sire breeds and relationships between terrain use and performance when daughters graze foothill rangelands as cows. Appl. Anim. Behav. Sci. 97, 105–121.

Voisinet, B.D., Grandin, T., Oconnor, S.F., Tatum, J.D., Deesing, M.J., 1997a. Bos indicus-cross feedlot cattle with excitable temperaments have tougher meat and a higher incidence of borderline dark cutters. Meat Sci. 46, 367–377.

Voisinet, B.D., Grandin, T., Tatum, J.D., O'Connor, S.F., Struthers, J.J., 1997b. Feedlot cattle with calm temperaments have higher average daily gains than cattle with excitable temperaments. J. Anim. Sci. 75, 892–896.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164–168.